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Response of boreal lakes to changing wind strength: Coherent physical changes across two large lakes but varying effects on primary producers over the 20th century

Kristin E. Strock,[1,a*] **Jasmine E. Saros**,[1] **Suzanne McGowan**,[2] **Mark B. Edlund**,[3] **Daniel R. Engstrom**[3]

[1]Climate Change Institute, University of Maine, Orono, Maine
[2]School of Geography, University of Nottingham, Nottingham, UK
[3]St. Croix Watershed Research Station, Science Museum of Minnesota, Marine on St. Croix, Minnesota

Abstract

Near-surface wind speeds have changed over recent decades, raising questions about the extent to which these changes are altering the vertical thermal structure of lakes and affecting lake food webs. Neo- and paleolimnological techniques were used to assess wind-driven changes in lake thermal habitat and resulting effects on primary producers in two lakes in Isle Royale National Park, an island archipelago located in Lake Superior, where wind speed has increased in recent decades. Responses in Siskiwit Lake, a large (16 km^2 surface area), deep (Z_{max} = 49 m), oligotrophic lake, were compared to those of Lake Desor, a moderately large (4.3 km^2) but shallower (Z_{max} = 13 m), mesotrophic lake. High-frequency sensor data suggested that changes in wind speed affected epilimnion thickness in both lakes synchronously ($\rho = 0.7$, $p < 0.001$). Diatom-inferred mixing depths suggested a coherent shift in both lakes to deeper mixing (an increase of 3 and 6 m) since 1920 ($\rho = 0.8$), which was correlated with an increase in regional wind speed during the 20th century at the decadal-scale in Lake Desor and Siskiwit Lake ($\rho = 0.6$ and 0.4, respectively). In Lake Desor, algal biomass declined as mixing deepened from 1920 to 1980, and then cyanobacteria and cryptophyte pigments increased from 1980 to present, a period of inferred stable and deep mixing. Algal pigment concentrations in Siskiwit Lake were unchanged as mixing depth deepened. Although changes in wind speed altered lake physical structure similarly, the ecological consequences of these changes differed between lakes and were most likely influenced by lake-specific variability in nutrient and light availability.

Climate change is affecting key variables that regulate the vertical thermal structure of lakes, resulting in coherent shifts in physical lake characteristics across varying spatial and temporal scales (Livingstone 2008). For example, increasing surface-water temperatures have been observed in over 100 large lakes, including Tahoe, Tanganyika, and Baikal, as air temperatures increased (Schneider and Hook 2010). In North America and Europe, evidence suggests that the onset of lake ice is occurring later in the fall and ice off is earlier in the spring (Hodgkins et al. 2002; Jensen et al. 2007), which is predicted to lengthen the period of stratification (Magnuson et al. 2004; Blenckner 2005). In addition to changes in air temperatures, wind speed is changing in recent decades in many regions (Klink 1999, Desai et al. 2009, Pryor et al. 2009, McVicar et al. 2008) and dissolved organic carbon (DOC) concentrations are increasing in many surface waters across the Northern Hemisphere (Monteith et al. 2007). Both wind speed and DOC concentration can be strong regulators of physical lake structure (Fee et al. 1996; Keller et al. 2006; von Einem and Graneli 2010). Here, we explore regional climate effects, in this case increasing wind speed, on lake habitat in two lakes located in Isle Royale National Park (ISRO) in Lake Superior and resulting effects on primary producers.

Changes in the depth of the surface mixed layer can alter the availability of cold water refuge required by certain fish species, influence nutrient cycling, and modify productivity and diversity of plankton (Matthews et al. 1985; De Stasio et al. 1996; Wilhelm and Adrian 2008). A recent global synthesis documented high variability in surface-water warming trends in lakes (O'Reilly et al. 2015). In northern Germany, the altered weather patterns associated with the North Atlantic Oscillation (NAO) had varying effects on water temperatures among lakes with different mixing regimes (a deep dimictic lake was the most sensitive to changes in the NAO

*Correspondence: strockk@dickinson.edu

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[a]Present address: Environmental Science Department, Dickinson College, Carlisle, Pennsylvania.

while a polymictic lake was the least sensitive) (Gerten and Adrian 2001). Even in studies that reported coherent increases in surface-water temperatures, the trends in lake mixing were still highly variable (King et al. 1999; Benson et al. 2000). Similarly, a recent study of more than 200 lakes in the northeastern United States found that since 1975, deep-water temperatures increased in half of the study sites but decreased in the other half (Richardson et al. 2017).

Changes in lake mixing depth require considerable changes in lake water clarity or in wind strength, depending on the size of the lake. Thermal stratification is regulated by wind in moderately large lakes (surface area greater than 5 km^2; Fee et al. 1996). In smaller lakes, both water clarity (Fee et al. 1996) and wind strength (von Einem and Graneli 2010) play a role, with the relative importance of these controls varying by region. For example, cooler surface-water temperatures and shallower mixing occurred in Clearwater Lake in Ontario (0.8 km^2 in size) as a result of reduced regional wind speeds and greater light attenuation resulting from the increased delivery of DOC from the watershed (Tanentzap et al. 2008). Recent syntheses support these mechanisms across broad spatial scales. In a study of 26 lakes across the globe, Kraemer et al. (2015) found that lake morphometry (including lake depth and surface area) was a better predictor of recent change in thermal stratification than trends in surface-water warming. In the northeastern United States, water clarity was cited as an important regulator of surface-water warming and as a result, increasing strength of thermal stratification in 231 lakes (with a median size of 1.4 km^2) (Richardson et al. 2017).

An important consequence of climate-mediated changes in lake mixing is the direct (changes in temperature) and indirect (altered light and nutrient availability) effects on the productivity and diversity of primary producers. Warming increases metabolic rates, but more strongly for secondary vs. primary producers, theoretically leading to increased consumer-grazing pressure and reduced algal biomass (as demonstrated in experiments in estuarine environments by O'Connor et al. 2009). However, warming-induced changes in consumer pressures were only present with sufficient nutrient resources (O'Connor et al. 2009). It follows that the indirect effects (altered light and nutrient availability) and direct effects of climate-induced changes in lake mixing may interact in complex ways.

Models developed by Diehl et al. (2002) suggest that the relationships between light availability, nutrients, and mixing depth depend on a variety of factors, including abiotic light absorbents, nutrient enrichment, and source of nutrient supply. If changes in lake mixing result in greater oxygenation of the hypolimnion (e.g., Scully et al. 2000), internal nutrient cycling may be reduced. Alternatively, if changes in lake mixing intensify hypolimnetic anoxia, internal nutrient cycling can increase. This was observed in the Lower Lake of Zurich, where climate-induced changes in lake mixing resulted in increased hypolimnetic hypoxia and increased internal cycling of phosphorus despite reduced external phosphorus loading (North et al. 2014). Across the entirety of Lake Zurich, phosphorus levels are declining; however, the harmful cyanobacterium *Planktothrix rubescens* has increased in abundance (Posch et al. 2012). This shift in the primary producer community is attributed to altered thermal stratification in conjunction with changing nutrient ratios (Posch et al. 2012).

Shifts in phytoplankton community and diversity have been linked to changes in lake mixing and the resulting effects on light and nutrient availability (Gerten and Adrian 2002; Jäger et al. 2008; Wilhelm and Adrian 2008; Winder and Hunter 2008); however, there is marked variability in phytoplankton community response within and across regions. For example, despite a strong relationship between air temperature and changes in surface-water temperature in boreal lakes across Ontario, there were only weak relationships between this climate-mediated change and plankton (Arnott et al. 2003). Instead, there was a high amount of variability in richness and abundance of plankton both within and among different regions in this study. It follows that intrinsic lake properties may mediate lake response to climate-driven changes in lake mixing such that lakes in the same region and experiencing similar climate forcing may have different ecological responses to this disturbance over time (e.g., Stone et al. 2019).

Research in other boreal lakes suggested that deepening mixed layers can increase production by algae, with diatoms, dinoflagellates, chrysophytes, and chlorophytes responding more strongly to this change (Cantin et al. 2011). In contrast, Berger et al. (2010) found that total phytoplankton production was unaffected by deepening mixed layers, but was stimulated when the mixed depth became shallower. In various lakes across the globe, phytoplankton biomass has increased, decreased, and remained unchanged as surface-water temperatures warmed (summarized by Bayer et al. 2016). This large amount of variability may confound our ability to accurately predict the effects of climate-mediated changes in lake mixing on algae, the base of the aquatic food web.

In a review of climate change effects on lake thermal properties, Livingstone (2008) suggested that understanding the large-scale impacts of climate change on physical lake habitat will require additional research on lake mixing over various time scales. Paleolimnological tools developed by Saros et al. (2012) can provide long-term records of lake mixing and put modern changes in the context of past variability. Here, we used both high-frequency lake temperature data and paleolimnological tools to better understand regional climate effects; in this case, increasing wind on lake habitat in two lakes located in ISRO. ISRO is a remote island archipelago in the northwest corner of Lake Superior. Wind speeds have increased in this region in recent decades (Desai et al. 2009), which could have strong effects on the physical habitat of large lakes. We used mixing depth optima for three diatom indicator taxa to reconstruct lake mixing depth in two lakes over the last century and fossil algal pigments to understand the effects of altered lake mixing on primary producers. We expected lake mixing depths to deepen synchronously across the two lakes due to the strong effect of wind on mixing depth in lakes greater than ~ 5 km^2 (Fee et al. 1996) and algal production to increase uniformly across algal groups when lakes mixed more deeply, as was observed by Diehl et al. (2002) in low turbidity systems.

Site description

ISRO is an island archipelago 2314 km^2 in size and comprised of one main island and numerous fringing islets, located in northwest Lake Superior (Fig. 1). Aquatic environments (wetlands, lakes, and rivers) cover 80% of the park area and support diverse native fish populations that have long been a cultural resource for the area and supported active fisheries for lake trout, northern pike, and several other species. The island also has a history of copper mining (both native and Euroamerican), which varied in intensity over time and ended by the late 1800s (Shelton 1997). Accessible only by boat or seaplane, ISRO lake ecosystems are designated as Class I Wilderness due to relatively pristine and undisturbed landscapes. As a result, these boreal lake ecosystems are high priorities for protection and conservation.

The bedrock geology of the island consists of a series of basaltic lava flows interlayered with sedimentary rocks (sandstones and conglomerates) (Thornberry- Ehrlich 2008). Glacial till and erratics are scattered across the island, with abundant glacial till deposits on the southwest end of the island that covers most bedrock. The terrestrial ecosystem is in a transitional zone between northern hardwood and southern boreal forests, with dominant species of white birch, quaking aspen, white spruce, balsam fir, and tag alder (Stottlemyer et al. 1998). Lakes on the island are typically mesotrophic; however, Siskiwit Lake, ISRO's largest lake, is oligotrophic with low nutrient concentrations and algal biomass (Table 1). The lakes have alkaline pH values ranging from 7.5 to 8.7 and DOC concentrations ranging from 4 to 7 mg L^{-1}. Of the two study lakes, Siskiwit Lake is considerably larger (16 km^2) and deeper (maximum depth of 49 m) compared to Lake Desor (4.3 km^2 in size and a maximum depth of 13 m).

Methods

High-frequency temperature data collected in the summer of 2012 were used to compare epilimnion depth in both Siskiwit and Desor lakes. Stratification metrics were correlated with daily regional wind speed data. To assess whether increasing regional wind speeds are driving similar long-term changes in lake mixing depths across the large lakes of ISRO, changes in diatom-inferred

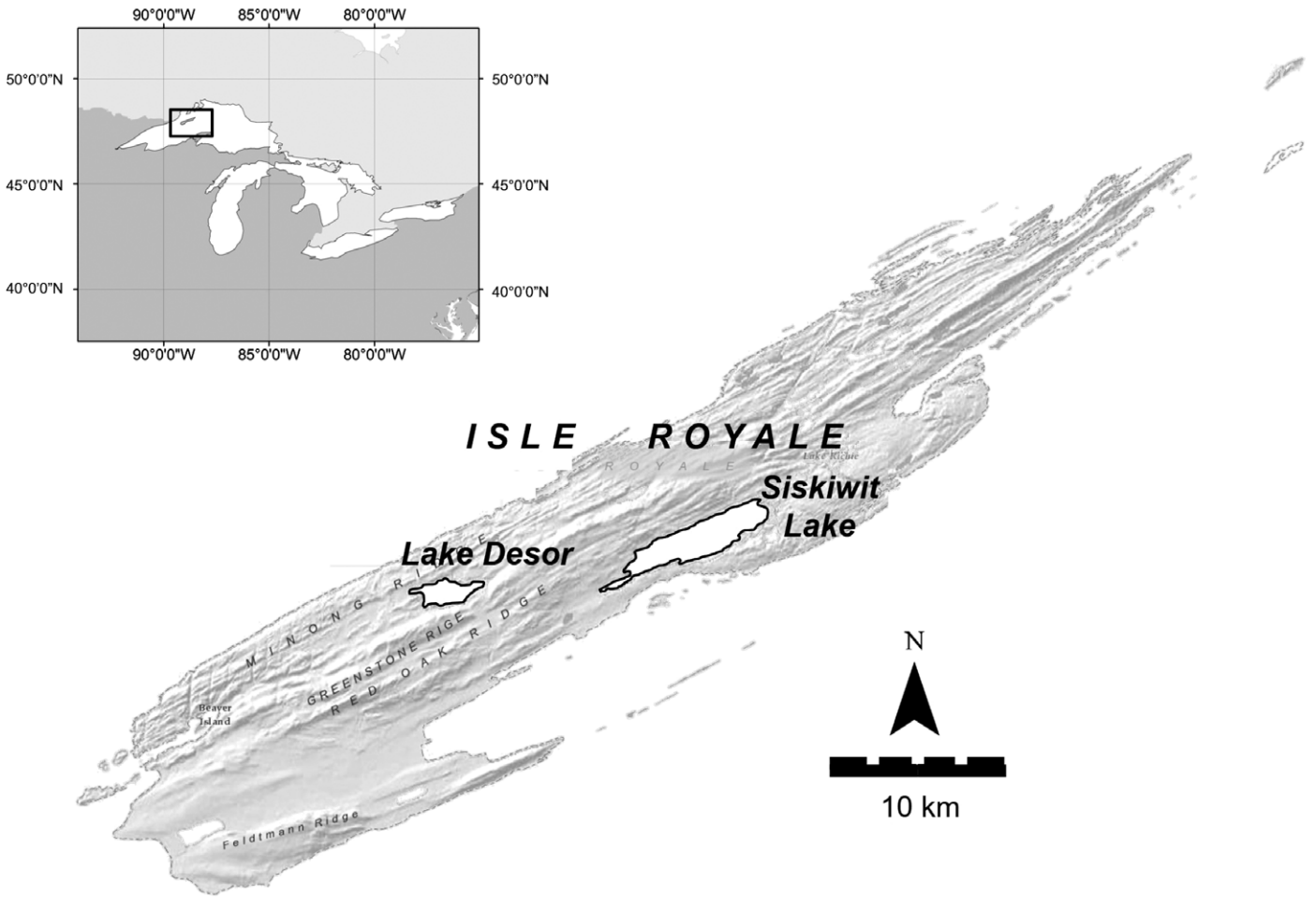

Fig. 1. Map of Isle Royale National Park, an island archipelago located in the northwest corner of Lake Superior. The two lakes included in this analysis, Siskiwit Lake and Lake Desor, are outlined in black.

Table 1. Morphometric and mean chemical data for lakes included in this study.

Lake	Max depth (m)	Area (km^2)	pH	Chl *a* ($\mu g\ L^{-1}$)	Total Phosphorus ($\mu g\ L^{-1}$)	Total Nitrogen ($\mu g\ L^{-1}$)	DOC ($mg\ L^{-1}$)	SO_4 ($mg\ L^{-1}$)	Secchi (m)
Siskiwit	49	16	8.0 (0.04)	0.9 (0.1)	4 (0.4)	214 (7.0)	5.8 (0.1)	5.0 (0.3)	7.6 (0.3)
Desor	13	4.3	8.3 (0.03)	2.4 (0.2)	12 (0.3)	444 (4.0)	7.8 (0.5)	3.8 (0.1)	2.9 (0.2)

Chemical values are mean values during June–August of 2008 and 2009 with SE in parentheses. Data from Elias (2009) and Elias and Damstra (2011).

mixing depth in the sediment records of Desor and Siskiwit lakes were compared to each other and to modeled values of surface wind speed for the past century. Due to the relatively slow sedimentation rate of Siskiwit Lake, correlations in the sediment record were performed at the decadal-scale. To determine how changes in lake mixing could affect the base of the aquatic food web, fossil algal pigment concentrations were quantified in both lakes.

High-frequency lake water temperature

Temperature loggers (Onset HOBO® Pendant UA-002) were deployed in Siskiwit and Desor lakes to monitor changes in lake stratification throughout the open water season in 2012. Loggers were deployed on a vertical cable at 1 m intervals from 1 m below the surface to 1 m above the sediment in Lake Desor and to a depth of 18 m in Siskiwit Lake. Loggers did not extend throughout the entire water column of Siskiwit Lake; however, monitored depths spanned the epilimnia, metalimnia, and hypolimnia in each lake. Temperature data were recorded every hour. Daily averages of hourly data were calculated for each depth and used to calculate the thickness of the epilimnion every day throughout July and August. The epilimnion thickness was defined as the region above the first depth where there was at least 1°C change in temperature per meter. When surface forcing resulted in weak stratification in the top 2 m of the lake (which only occurred in ~ 6% of measurements), the epilimnion thickness was defined as the region above the depth of maximum temperature change (Wetzel 1975). Wind speed data from the National Oceanic and Atmospheric Administration's ROAM 4 buoy, which is located at the southwest corner of the island and is the closest wind speed record (1996 to present) to the study lakes, were used to relate daily epilimnetic thickness to surface wind speed using Spearman's rank correlation coefficient.

Paleolimnology: Sediment core collection and dating

Sedimentary diatom and algal pigment records were used to reconstruct lake mixing depth and algal community change, respectively, over the last century. Sediment cores were collected from Siskiwit Lake in 2009 and Lake Desor in 2011 by boat with a Pylonex HTH gravity corer from the deepest point in the lake. Methods detailing collection and analyses for the Siskiwit Lake sediment core can be found in Saros et al. (2012). The Lake Desor core was 50 cm in length and was subsampled in the field in 0.5 cm increments until 20 cm and then 1 cm increments to 50 cm. The first 200 yr of each core were dated using ^{210}Pb methods. ^{210}Pb activities were measured by alpha spectrometry (modified from Eakins and Morrison 1978 for 16 intervals covering the past ~ 200 yr). Dates were calculated based on the constant rate of supply (CRS) model (Appleby 2001).

Paleolimnology: Diatom-inferred lake mixing depth index

Sediment subsections were treated with 10% HCl and 30% H_2O_2 to digest carbonate and organic matter. The processed samples were settled onto coverslips and mounted onto slides with Naphrax. At least 300 diatom valves per slide were counted on an Olympus BX-51 microscope with differential interference contrast under oil immersion at × 1000 magnification. Diatom taxonomy was based primarily on Krammer and Lange-Bertalot (1986–1991) and Camburn and Charles (2000). Updated naming conventions were obtained from Diatoms of North America (https://diatoms.org/).

The mixing depth model developed by Saros et al. (2012) was applied to the diatom profile to reconstruct mixing depth over time. This method utilizes known diatom ecological preferences of three diatom indicator species: *Lindavia bodanica* (Grunow) Håkansson, *Lindavia comensis* (Grunow) Nakov, and *Discostella stelligera* (Cleve & Grunow) Houk & Klee. These preferences were determined from lake surveys and assay experiments in order to provide an optimal mixing depth (depth to the thermocline) for each species (Saros et al. 2012). The mixing depth index (MDI) is calculated by applying calculated optima to the relative abundances of the three target species (within the full assemblages) using the following weighted-averaging equation (Birks 2010):

$$\hat{x}_i = \frac{\sum_{k=1}^{m} y_k u_k}{\sum_{k=1}^{m} y_k}$$

where $\hat{x}_i$, the inferred value for mixing depth; y_k, the abundance of taxon k in the fossil sample; and u_k, the mixing depth optima of taxon k for species 1 (= k) through m. The mixing depth optimum for *L. bodanica*, *L. comensis*, and *D. stelligera* are 14 m, 9 m, and 4 m, respectively (Saros et al. 2012). For the mixing depth inference model, the root mean square error of prediction, estimated by comparing measured to reconstructed mixing depths for 17 lakes, was 3.8 m, with an r^2 of 0.26 (Saros et al. 2012).

The MDI for Siskiwit and Desor lakes were analyzed for the past 150 yr for synchronous changes in mixing depth with

Spearman's rank correlation coefficient (Patoine and Leavitt 2006). Because temporal resolution varied along the time series and between lakes, estimates of mixing depth synchrony were at decadal scales of coherence. This resulted in nine samples to compare in each core (an average value for each decade from 2000 to 1910, excluding 1940 where there were no data available). Where the sedimentation rate was higher and there were multiple samples in one decade, values were averaged to obtain one decadal value. In addition to being compared to each other, Lake Desor and Siskiwit Lake MDI were correlated to surface wind speed data from the NOAA-CIRES 20th century climate reanalysis (Compo et al. 2011) using the Spearman's rank correlation coefficient. Annual wind speed data were also averaged into decades for comparison to paleolimnological data. Although correlations were higher when comparing MDI to only summer months (average wind speeds in June, July, and August) in some instances, we felt comparisons to annual wind speed were a better reflection of the conditions preserved in the sediment record. Air temperature data collected at the Mott Island weather station on ISRO were compared to air temperature from long-term reanalysis products, including National Center for Environmental Predication/National Center for Atmospheric Research V1 Model (NCEP V1) (Kalnay et al. 1996) and the Parameter-elevation Regressions on Independent Slopes Model (PRISM) (PRISM Climate Group and Oregon State University 2004), from 1950 to present (data accessed from Climate Reanalyzer, Climate Change Institute, University of Maine, U.S.A.). The NOAA-CIRES 20th century climate reanalysis was chosen because it most closely resembled the modern weather station data collected at ISRO with an average deviation of predicted vs. observed temperatures of 0.1°C (as compared to > 3°C for both NCEP V1 and PRISM models). Only reanalysis models that provided wind data that spanned the 20th century (1871–present) were considered.

A detrended correspondence analysis (DCA) was used to quantify the dominant pattern of down-core diatom assemblage variability. The DCA was performed using Hellinger transformed diatom species data using all taxa with greater than 5% relative abundance (Legendre and Gallagher 2001). All statistical analyses were conducted using the R software (version 2.12.1, R Development Core Team 2011) and the rioja package (Juggins 2012).

Paleolimnology: Fossil algal pigments

To better understand the biotic implications of changes in lake mixing depth, fossil algal pigments were used to provide a record of lake production and primary producer community structure. Pigments were isolated using high-performance liquid chromatographic separations of chlorophylls, carotenoids, and their derivatives (Leavitt and Findlay 1994). Pigments isolated from sediments were identified by spectral characteristics and chromatographic mobility by comparison with those from commercial pigment standards (DHI Denmark) (Chen et al. 2001). Principal component analysis (PCA) was used to quantify variability in the suite of fossil pigments detected in each core. Pigment abundances were log-transformed ($x + 1$) to normalize the data and labile pigments (fucoxanthin, chlorophyll *a*, and its derivatives) were excluded to minimize the influence of pigment degradation.

Results

High-frequency lake water temperature

The onset of stratification occurred in the first week of July in 2012 for both Siskiwit and Desor lakes with a maximum temperature difference between the epilimnion and hypolimnion in the middle of July for Siskiwit Lake and the last week of July for Lake Desor (Fig. 2). The depth of the epilimnion extended to 9 m in both lakes. Erosion of the epilimnion began in early August and continued throughout the month. The thicknesses of the epilimnia in the two lakes were positively correlated with one another throughout the summer ($\rho = 0.71$, $p < 0.001$). The thickness of the epilimnion in Lake Desor was positively correlated with daily average wind speed measured at Lake Superior weather stations ($\rho = 0.29$, $p = 0.04$). Siskiwit Lake was less strongly correlated with wind speed ($\rho = 0.20$, $p = 0.16$). The epilimnion thickness increased on days with higher wind speed.

Paleolimnology: Sediment core collection and dating

The ^{210}Pb profile for Lake Desor had an exponential decline in ^{210}Pb activity from the surface to bottom sediments. There was a slight disruption in this trend for the top 10 cm that could suggest some sediment mixing; however, the error in the dating model in the top 10 cm was only ± 1.5 yr on average (Fig. 3a). The ^{10}Pb profile for the Siskiwit Lake sediment core can be found in Saros et al. (2012).

Paleolimnology: Diatom-inferred lake MDI

Several general trends emerge in the sedimentary diatom profile from Lake Desor (Fig. 4). *Aulacoseira* species were present throughout the record and made up 10–20% of the diatom assemblage. *L. comensis* was absent or made up less than 1% of the assemblage prior to 1970, but its abundance increased from 1970 to present where it accounted for up to 30% of the assemblage in 2000. The increase in *L. comensis* occurred as the relative abundances of *D. stelligera* declined. Relative abundances of *L. bodanica* were low throughout the record. *Cyclotella atomus* increased slightly from 1970 to 2000; however, abundances remained below 10% until recent years when the abundance more than doubled. *Fragilaria crotonensis* increased from less than 5% relative abundance to 10% around 1920 and remained at 10% until 1970 when abundances declined to approximately 5% and remained at that level until present. Smaller *Fragilaria* taxa sensu *lato* (e.g., *Staurosirella*, *Staurosira* spp.) increased slightly in abundances (from below 5% to just under 10%) around 1950–1960. Trends in diatom change (DCA Axis 1 score in Fig. 5) suggest the composition of the assemblage began to change around 1960 and then stabilized from 1980 to present.

Lindavia bodanica had low overall abundance throughout Lake Desor's sediment core, and declined slightly in the past two decades as compared to the last century (Fig. 5). *L. comensis* made up less than 1% of the algal assemblage in the early part of the

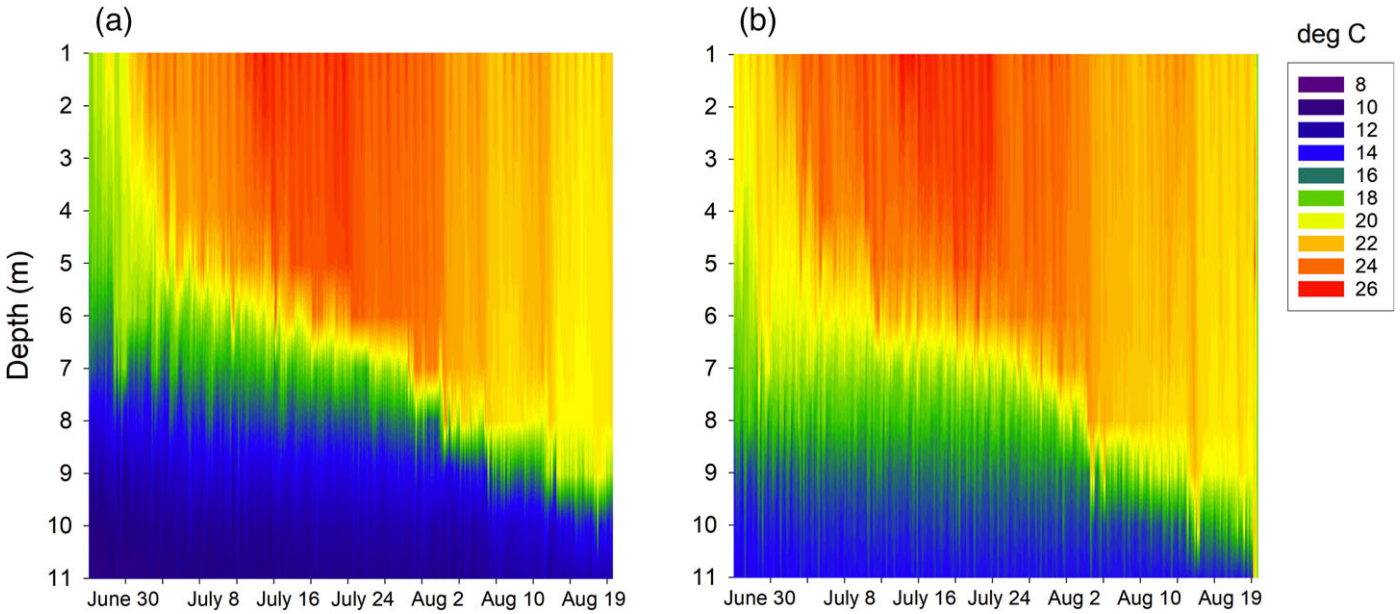

Fig. 2. Hourly temperature data collected from sensor arrays deployed at 1 m intervals in Siskiwit (**a**) and Desor (**b**) lakes for July and August of 2012. Note only top 11 m of the water column is shown for both lakes.

century, but increased steadily from the 1960s to 2000 when it made up over 30% of the total assemblage. During the period of rapid increase in *L. comensis*, *D. stelligera* declined in abundance and made up less than 1% of the diatom assemblages in recent years. The directional increase in *L. comensis* and decrease in *D. stelligera* produced an overall deepening in diatom-inferred mixing depth (Fig. 5). Present-day inferences suggest a lake mixing depth of 9 m in Lake Desor, which is in agreement with our direct monitoring of late summer lake thermal stratification (9–10 m; Fig. 2). The deepening of the diatom-inferred mixing depth began around 1960 in Lake Desor when *L. comensis* increased in abundance and the composition of the entire diatom community,

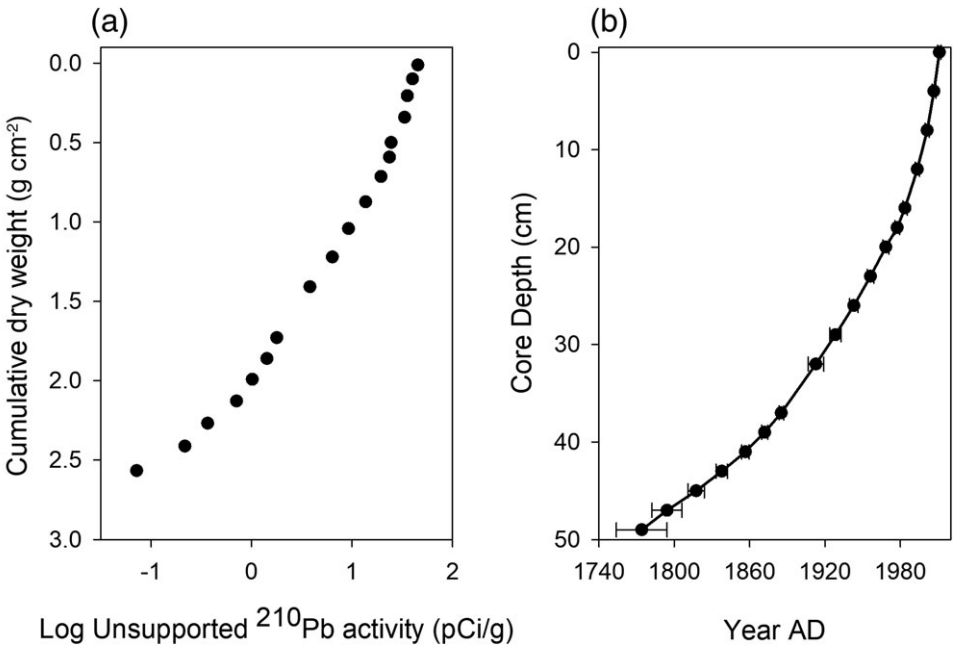

Fig. 3. Age model for the Lake Desor sediment core: (**a**) log unsupported ^{210}Pb activity and cumulative dry weight of sediment; (**b**) the age-depth profile based on the CRS model (Appleby 2001). Error bars, shown for the age of the dating model (**b**), represent $\pm$ 1 SD propagated from counting uncertainty.

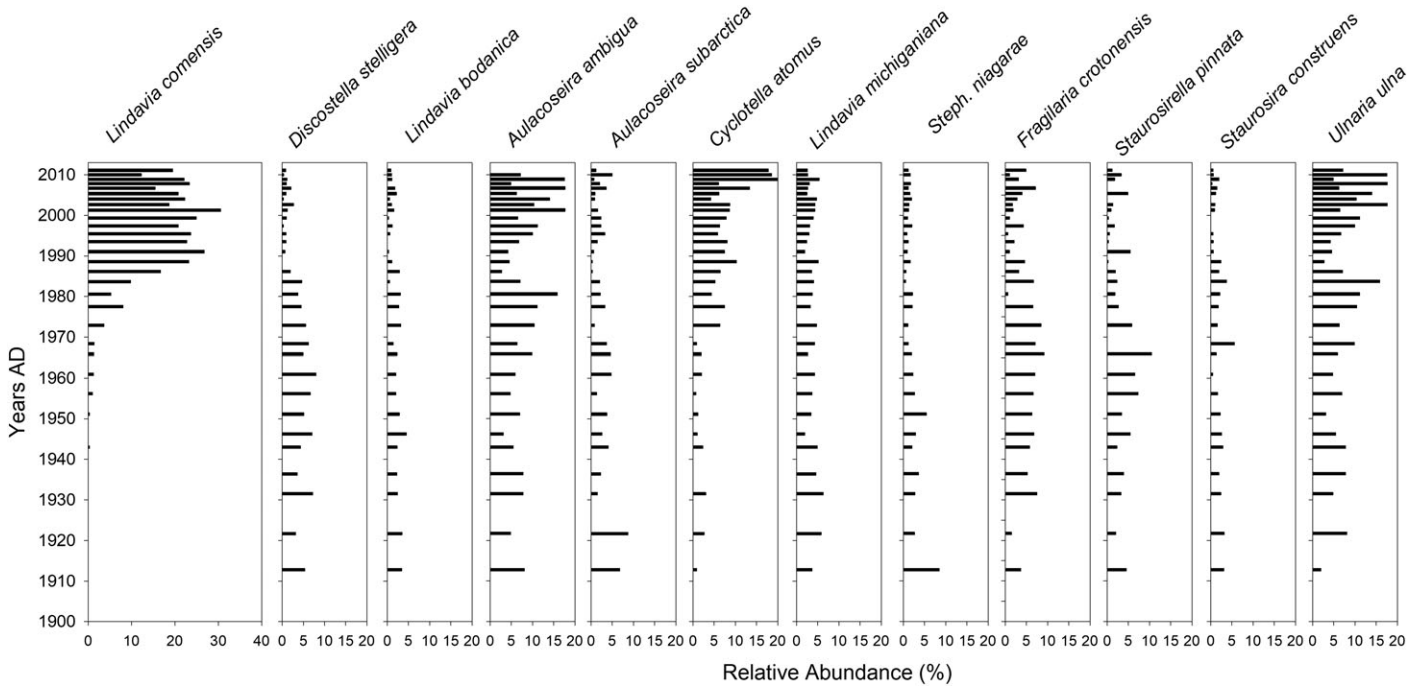

Fig. 4. Sedimentary profile of the relative abundances of dominant diatom taxa in Lake Desor during the 20th century.

represented by the DCA Axis 1 scores, also shifted (Fig. 5). The overall average mixing depth for the last century was 8 m. From the mid-1980s to present, the diatom-inferred mixing depth was consistently deeper than the overall average and was stable during this time. There was a greater amount of variability in mixing from 1900 to 1950, with values fluctuating between 6 and 7 m. From the early 1900s to 2010, lake mixing depth increased by more than 50%. This shift in mixing depth (from 6 to 9 m) is within the root mean square error of prediction (3.8 m) for the diatom-inferred lake mixing model (Saros et al. 2012).

Diatom-inferred lake mixing records from Desor and Siskiwit lakes were synchronous ($\rho = 0.8$, $p = 0.01$) at the decadal-scale throughout the past century (Fig. 6). When compared to the wind reanalysis for the region, Lake Desor had a significant correlation between lake mixing and wind speed at the decadal-scale ($\rho = 0.6$, $p = 0.05$) and was more highly correlated with wind than the Siskiwit Lake record ($\rho = 0.4$, $p = 0.09$). There is a significant linear increase in wind speed from 1870 to 2010 (shown as a solid red line in Fig. 6, $p < 0.001$). The simple linear regression from 1985 to 2010 (the period studied by Desai et al. (2009)) is not significant (shown as a dashed red line in Fig. 6, $p = 0.14$). The reanalysis data used here suggest an increase of 0.013 m s^{-1} yr^{-1} as compared to 0.22 m s^{-1} yr^{-1} across Lake Superior reported by Desai et al. (2009). Lake mixing records from both lakes track regional wind speed in the first half of the 1900s but depart from the trends in wind during the most recent decades as diatom-inferred mixing depth remained stable from 1980 to present in Lake Desor and continued to deepen in Siskiwit Lake.

Paleolimnology: Fossil algal pigments

Fossil algal pigments were used to assess changes in the algal standing crop and community composition over the time period that mixing depth changed in both Desor and Siskiwit lakes. Siskiwit Lake had low overall concentrations of algal pigments throughout the record, and there was little to no change in the pigment assemblage or in the organic content of the sediment (Fig. 7a). The pigment record from Lake Desor suggested an overall decline in algal standing crop as diatom-inferred lake mixing depths deepened from 1960 to 1980 (Fig. 7b). The decline in diatoxanthin (diatoms) preceded mixing depth changes, with a decline beginning approximately in 1920. The average carotenoid pigment concentration was at its lowest level in 1980 (20 nmol g^{-1} organic carbon) and half of the overall average for the period of record (1800–2010 A.D.) (Fig. 7b). During the last two decades, when mixing depth was deeper and more stable, the overall average of carotenoid pigments increased. The sediment organic content increased from 1950 to present. The increase in average carotenoid pigments was primarily driven by an increase in alloxanthin (cryptophytes), zeaxanthin (cyanobacteria), and β-carotene from 1980 to present. Diatoxanthin (diatoms) stabilized in recent decades, while canthaxanthin (colonial cyanobacteria) continued to decline from 1980 to present, resulting in recent concentrations that were the lowest for the entire period of record. The PCA scores for axis one track the decline in carotenoid pigments from 1920 to 1980 and subsequent increase in zeaxanthin (cyanobacteria) and alloxanthin (cryptophytes) from 1980 to present.

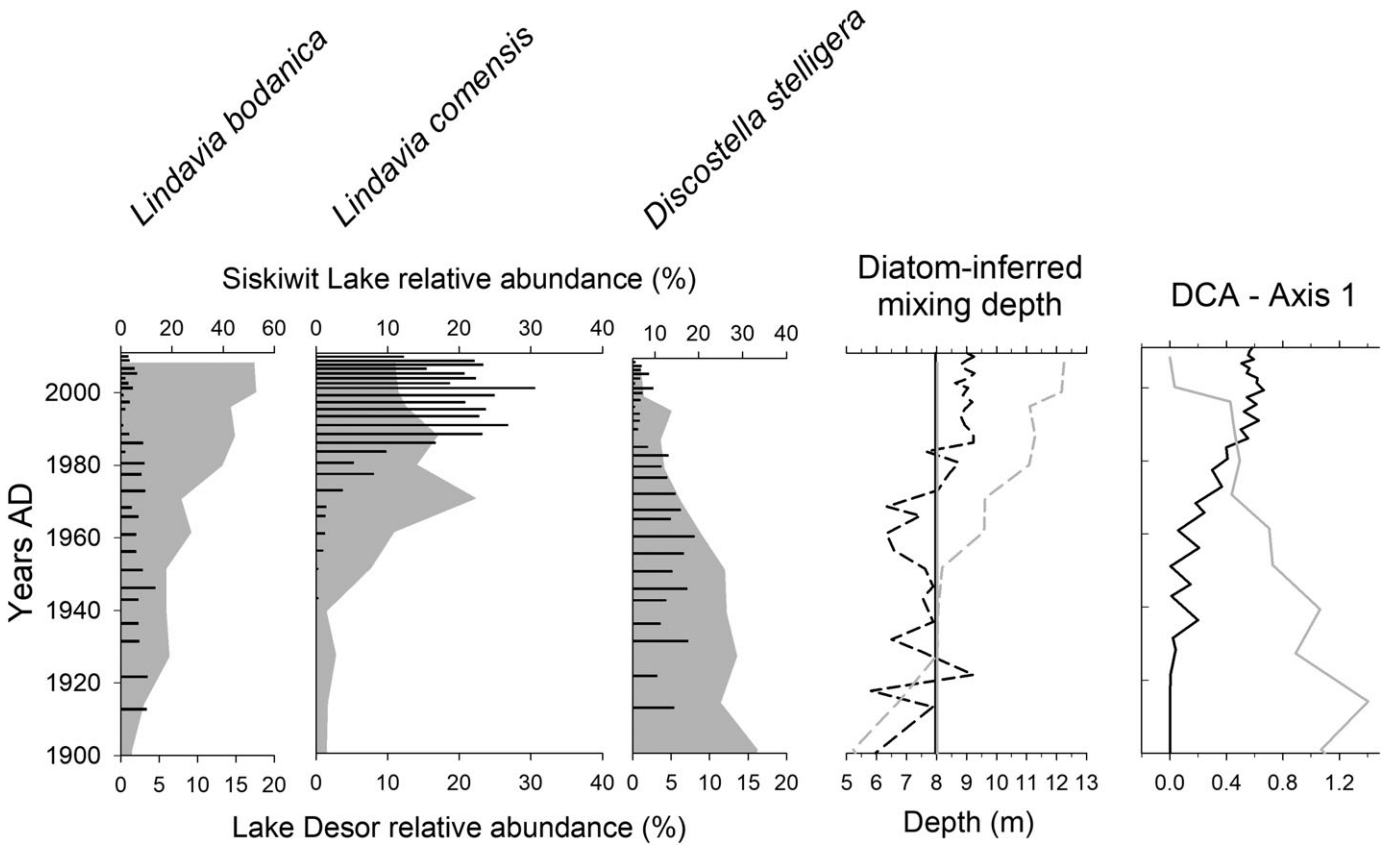

Fig. 5. Lake Desor (black) and Siskiwit Lake (gray) sediment profiles of the relative abundance of the three diatom taxa used to infer lake mixing depth, reconstructed lake mixing depth, and the DCA of the entire diatom assemblage shown at right. Scales for Siskiwit Lake (top of plots) differ for those in Lake Desor (bottom of the plots). The vertical line on the mixing depth plot is an overall average for the period of record for Lake Desor (black) and Siskiwit Lake (gray). Siskiwit Lake data are modified from Saros et al. (2012).

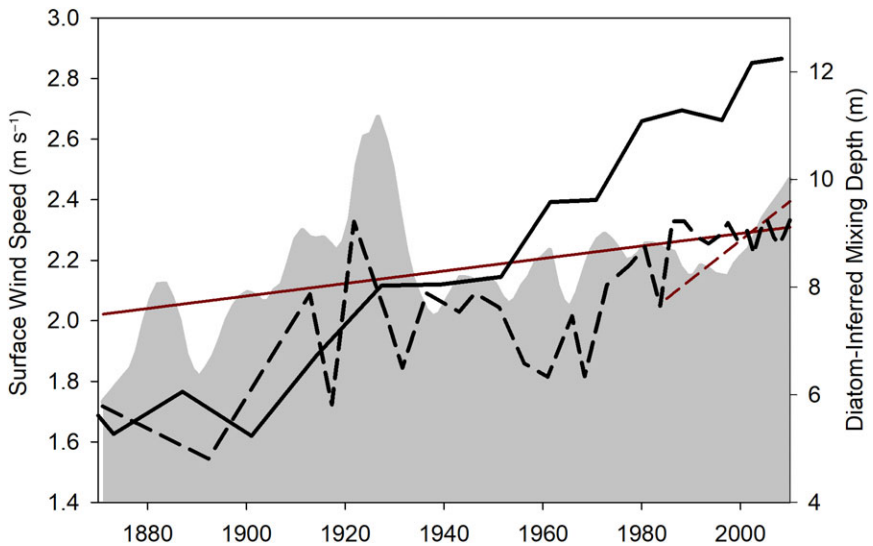

Fig. 6. Diatom-inferred lake mixing depth records for Siskiwit (solid black line) and Desor (dashed black line) lakes in comparison to regional wind speed (gray) from the NOAA-CIRES 20th century climate reanalysis (Compo et al. 2011). Wind data were graphed as locally weighted regression scatterplot smoothing (LOESS) trends; however, all correlations which compare wind speed and diatom-inferred lake mixing depth used the mean annual wind speed calculated for each decade. The solid red line indicates a simple linear regression of wind data throughout the 20th century. The red dashed line is a simple linear regression of wind data from 1985 to present.

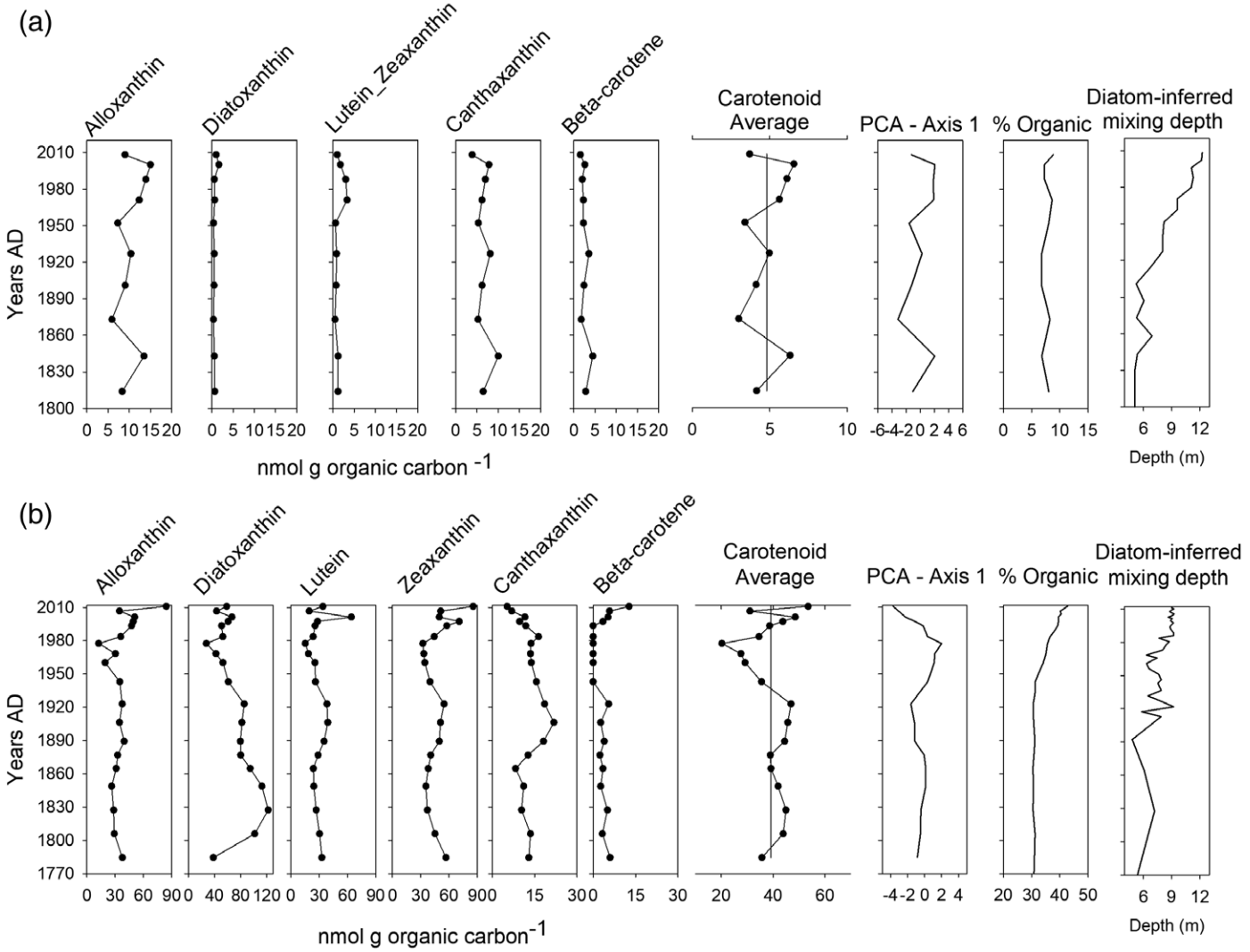

Fig. 7. The sedimentary record of fossil pigments, PCA axis 1 score for all pigments detected, and the percentage of organic material in (**a**) Siskiwit Lake and (**b**) Lake Desor. Pigment concentrations are expressed per gram organic matter and represent cryptophytes (alloxanthin), diatoms (diatoxanthin), green algae (lutein), cyanobacteria (zeaxanthin), colonial cyanobacteria (canthaxanthin), and most algae and land plants (β-carotene). In the Siskiwit Lake core, lutein and zeaxanthin were inseparable during detection and are summed together. The vertical line on the plot of the concentration of carotenoid pigments is an overall average for the period of record for each lake. Diatom-inferred mixing depth plots are also presented here for reference.

Discussion

Siskiwit and Desor lakes had coherent deepening of lake mixing depth as wind strength increased over the 20th century. Diatom-inferred changes in lake stratification began around 1920 in Siskiwit Lake and record a steady deepening of lake mixing over time. In Lake Desor, changes in lake stratification begin around 1960 and record deepening of lake mixing for two decades followed by stable deep mixing until present. Both lakes had synchronous changes in daily epilimnion thickness throughout the summer of 2012, suggesting that wind affected epilimnion thickness similarly in the seasonal and decadal records. Over the past century, changes in the mixing depth of Siskiwit Lake, the larger, deeper, and clearer lake, were of a greater magnitude (doubling of lake mixing depth) than those in Lake Desor. Higher DOC concentrations in Lake Desor may have moderated climate-induced warming, as predicted in simulations by Rose et al. (2016), and thereby dampened changes in lake mixing compared to Siskiwit Lake. Although both lakes responded similarly to regional changes in wind over the last century, they differed in the subsequent effects on algae. Deeper lake mixing temporarily reduced algal biomass in Lake Desor but had no discernable effect on abundance of primary producers in Siskiwit Lake, as inferred by sedimentary pigments. This would suggest that changes in wind altered physical lake properties similarly during the 20th century, but that the resulting effects on primary producers were lake-dependent.

We compared diatom-inferred lake mixing depth to reanalysis estimates of wind speed every decade throughout the 20th

century. However, comparisons by Desai et al. (2009) found that regional reanalysis estimates of wind speed underestimated the increase in wind speeds over Lake Superior by nearly half, suggesting that comparisons to reanalysis data may underestimate the full magnitude of historical increases in wind speed over Siskiwit and Desor lakes. This was the case in our comparison of simple linear regression trends from 1985 to 2010, where the increase in reanalysis estimated wind speed was an order of magnitude less than that reported by Desai et al. (2009). As a result, comparisons from the sediment record to historical wind speed estimates are useful for comparing general trends and direction of change but may differ in the actual magnitude of change.

An increase in lake mixing depth is counter to model predictions for regions experiencing a decrease in regional wind speeds as opposed to an increase. Projections for large lakes in the Upper Great Lakes region predicted that lake mixing patterns will experience little or no change over time (Fee et al. 1996; Magnuson et al. 1997) or slightly shallower and stronger stratification (De Stasio et al. 1996). Recent modeling of changes in lake habitat in the Great Lakes region supports these projections with an increase in the frequency and duration of stratified conditions in deep lakes (Edlund et al. 2017). Similarly, more than 200 lakes in the northeastern United States recorded increased lake surface-water temperatures and increased strength of thermal stratification since 1975 (Richardson et al. 2017). These studies consider the direct effects of warming air temperatures on lake temperature and thermal stratification and indirect effects where long-term warming has also led to a shorter duration of ice cover in lakes (Sharma et al. 2016). Changes in ice duration can lead to a longer stratified period and/or stronger thermal stratification, which has been linked with shifts in phytoplankton and bacterial communities in lakes (Beall et al. 2016). Another key factor that has been linked to shallower and/or stronger thermal stratification is reduced water clarity in recent decades due to increased DOC concentrations (Strock et al. 2017; Pilla et al. 2018).

The disparity between our results studying lakes on an island archipelago and other studies in the Great Lakes Region is most likely due to the effects of large waterbodies on regional weather patterns. Lake Superior has warmed faster than the surrounding air due to decreased ice cover and increased heat input (Austin and Colman 2007; Desai et al. 2009). This has destabilized the atmospheric surface layer above the lake and resulted in an increase in surface wind speeds above Lake Superior (Desai et al. 2009), which is otherwise an anomaly in central North America, where wind speeds are declining across most inland regions (Klink 1999; Pryor et al. 2009). Similar reductions in wind speed have been observed in China, the Netherlands, the Czech Republic, and Australia (Smits et al. 2005; Xu et al. 2006; McVicar et al. 2008). These changes have been attributed to hemispheric warming trends (Xu et al. 2006), changes in circulation (Lu et al. 2007), and increased surface roughness due to increased vegetation (Vautard et al. 2010).

It follows that relatively large lakes ($> 5\ km^2$) that were experiencing a decline in wind speed would have the opposite trends in the diatom indicator taxa used in this study. This was the case in a compilation of sediment records from a number of lakes that ranged in size and spanned the Northern Hemisphere (Rühland et al. 2008). In this study, small *cyclotelloid* species, including *D. stelligera*, increased in relative abundance during the last century in arctic, alpine, and some temperate lakes, including Whitefish Bay in Lake of the Woods, Ontario, Canada. This large lake is located over 300 km inland from Lake Superior and ISRO along the border of Minnesota and Ontario, where wind speeds have been declining (Klink 2002). Similarly, diatom-inferred lake mixing depth became shallower in two large inland lakes in Maine, U.S.A., as wind speeds declined (Boeff et al. 2016). The changes in Whitefish Bay and other lakes were attributed primarily to increasing temperatures and a longer ice-free period, but the findings presented here suggest that wind-driven changes in lake mixing should also be considered an important driver of change.

In addition to the *cyclotelloid* species considered in this study, *Aulacoseira* species can also be used to infer changes in lake mixing depth over time (Wang et al. 2008; Stone et al. 2016). *Aulacoseira* species, which are often tychoplanktonic, are typically more successful in well-mixed settings where mixing helps these organisms to maintain their position in the photic zone (Lund 1954; Rühland et al. 2003). For example, *Aulacoseira* species and other meroplanktic algae were correlated more strongly with daily wind speed than any other environmental variable in Lake Apopka, Florida, U.S.A. (Carrick et al. 1993) and would be expected to increase in abundance when wind speeds increase. In Siskiwit Lake, there were relatively low abundances of *Aulacoseira* species throughout the sediment record and they exhibited relatively small changes in abundance over time (Supporting Information Fig. S2). In Lake Desor, *Aulacoseira ambigua* had higher relative abundances approximately in 1980, which declined until 1990 and then returned to higher abundances in the 2000s. Higher abundances in recent decades are consistent with increased wind speed over this time; however, this interpretation is complicated by the high amount of variability in the abundances of *A. ambigua* during this time.

Deeper lake mixing in Lake Desor had subsequent effects on lake habitat, evidenced by changes in the fossil algal pigment assemblage that were not detected in Siskiwit Lake despite similar changes in lake mixing depth over time. The differences in algal community response to deeper lake mixing may be attributed to differences in water transparency and thus light limitation. The concentration of carotenoid pigments deposited in the sediment record dropped below the average concentration approximately in 1950 and continued to decline as mixing depths deepened in Lake Desor (~ 1960–1980). When increased wind drives the epilimnion depth deeper than the euphotic zone (the depth where 1% of the surface irradiance remains), phytoplankton growth will be increasingly limited by light (Jones et al. 1996) and net phytoplankton growth can be negative (Houser 2006). In Lake Desor, the euphotic zone extends to approximately 5.8 m (estimated by doubling the Secchi disk transparency, an approximate conversion factor for

clear lakes developed by Koenings and Edmundson 1991). This is considerably shallower than the modern thickness of the epilimnion (9 m) and would suggest that there is a large amount of area in the epilimnion that is light limited. Increased light limitation may have temporarily reduced the algal standing crop in Lake Desor. Similar findings were reported in small lakes in southern Sweden, where increased wind deepened lake mixing, while increased DOC concentration reduced the depth of the euphotic zone, resulting in an increase in light limitation (von Einem and Graneli 2010). This is not the case for Siskiwit Lake, which has an approximate euphotic zone depth of 15.2 m and a mixing depth of 9 m. This would suggest that light limitation is a stronger constraint on phytoplankton in Lake Desor. Increased light availability in Siskiwit Lake could also increase the susceptibility of pigments to photo-oxidation, which may have contributed to lower overall concentrations in the sediment record.

Changes in lake mixing can differentially alter the availability of nutrients among lakes. Deeper thermoclines can lead to greater oxygenation of the hypolimnion and reduced anoxia at depth (Scully et al. 2000), which could reduce sediment phosphorus release. Lake Desor is shallower than Siskiwit Lake, 13 m compared to 49 m, and experiences periodic anoxia in the hypolimnion (Kraft et al. 2010). In this case, deeper mixing may have led to reduced anoxia and diminished sediment phosphorus release, resulting in decreased algal biomass while mixing deepened. However, prolonged, deep mixing could subsequently increase the exposure of sediments to warm epilimnetic waters, which could increase mineralization rates and associated nutrient release (Liikanen et al. 2002). Increased vertical mixing would then make these hypolimnetic nutrients more available to epilimnetic plankton communities over time (Kristensen et al. 1992).

While mixing depths remained stable and deep from 1980 to present in Lake Desor, cyanobacteria and cryptophyte pigments increased in concentration. Cryptophyte species are motile and may have mixotrophic feeding strategies. Cryptophytes could benefit from deeper mixing because they have low light:nutrient needs and can capitalize on high bacterial biomass in the metalimnion (Ptacnik et al. 2003). An increasing frequency of cyanobacteria blooms has been observed in other lakes in ISRO in recent years, with *Lyngbya birgei* G.M. Smith, *Anabaena flos-aquae*, and *Anabaena planctonica* Brunnthaler as the three most prevalent bloom species (Edlund et al. 2011). Changes in water temperature and stratification have been suggested as possible mechanisms driving these changes (Edlund et al. 2017), but have yet to be directly tested.

It is unclear why the increase in cyanobacteria and cryptophyte pigments (~ 1980) may have lagged the deepening of lake mixing (~ 1960). These organisms may be responding to the direct effects of changes in lake water temperature, which may have accelerated in recent decades as changes in lake mixing stabilized in Lake Desor. This may be particularly important for cyanobacteria, which increase in dominance at warmer water temperatures (Kosten et al. 2012). At temperatures higher than 20°C, growth rates continue to increase in several cyanobacteria species despite reduced growth rates in most eukaryotic taxa (Paerl and Huisman 2008). In addition, we have described multiple ways in which changes in lake mixing may have altered the availability of nutrients in previous paragraphs. Multiple mechanisms may have been at play that altered the availability of nutrients differently over time. This is further complicated by the fact that cyanobacteria can dominate at low nutrient concentrations due to enzymes that can liberate phosphate from organic molecules (Coleman 1992) and to internal storages of phosphorus (e.g., Istvanovics et al. 1993) or in lakes with high algal biomass, which often occur with increased nutrient concentrations (Downing et al. 2001). Ongoing monitoring and experimental research could help to clarify the primary mechanisms linking deeper lake mixing with changes in algal biomass.

In addition to changes in climate during the 20th century, there has been an increase in the delivery of nitrogen to many lake ecosystems, even in remote regions of the Northern Hemisphere (Holtgrieve et al. 2011; Hobbs et al. 2016). Elevated atmospheric deposition of nitrogen from human sources can stimulate phytoplankton growth and alter community composition (Saros et al. 2003; Saros et al. 2005). There were no observable changes in productivity in Siskiwit Lake (inferred from fossil algal pigments), which suggests limited effects from nitrogen enrichment in this lake. In addition, there were variable changes in productivity in Lake Desor that included a decline in most algal taxa as mixing depths deepened. This is counter to the response typically associated with nutrient enrichment. The diatom indicator species used in this study respond to lake thermal structure when nitrogen is sufficient (Saros et al. 2012), which suggests that nutrient availability is critical to algal response to changing physical lake habitat. Continuing work is needed to clarify the role of nitrogen enrichment on phytoplankton community response to changes in physical lake habitat.

The response in Lake Desor differs from observations from a whole-lake mixing experiment (Cantin et al. 2011), in which a deepening mixed layer in boreal Lac Croche in Quebec led to an increase in productivity, with a strong response in diatom, dinoflagellate, chrysophyte, and chlorophyte abundance. Although Lac Croche has a similar maximum depth to Lake Desor and mixing was deepened to a similar depth, it is a smaller, clearer, and more oligotrophic lake. As mixing depth approached the depth at which 1% of incident light occurs in Lac Croche (~ 6–7 m), phytoplankton biomass began to decrease due to light limitation. In Lake Desor, which has higher DOC concentrations than Lac Croche, the depth at which light limitation occurred is shallower (~ 5.8 m) and the lake mixing depth was deeper (9 m as compared to 7.5 m). As a result, light limitation would be more severe in Lake Desor as compared to Lac Croche and may have contributed to the reduction in algal biomass in the former as mixing deepened.

Diatom-inferences suggest a shift to deeper lake mixing in Desor and Siskiwit lakes during the 20th century as wind speeds increased in this region. However, this change in lake mixing altered primary producers differently between the lakes. Although

Siskiwit Lake responded more strongly to climate-mediated changes in lake mixing (two times greater change in lake mixing depth than Lake Desor), there were minimal changes in algal standing crop as inferred by sedimentary pigments. Lake depth, clarity, and productivity appeared to be important characteristics that influenced how changes in lake mixing altered phytoplankton communities. When considering long-term biological response to changes in lake habitat, Lake Desor, the shallower and more productive lake, was a stronger sentinel of biological response to changes in lake mixing.

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Conflict of Interest

None declared.

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